

THE FOSSIL RECORD OF THE GLAREOLIDAE AND  
HAEMATOPODIDAE (AVES: CHARADRIIFORMES)

Storrs L. Olson and David W. Steadman

*Abstract.*—*Paractiornis perpusillus* Wetmore, a putative pygmy haematopodid from the lower Miocene of Nebraska, is shown to be a member of the Glareolidae and provides the first fossil record for the family as well as the first record from the New World. The fossil oystercatcher *Palostralegus sulcatus* Brodkorb, from the middle Pliocene Bone Valley Formation of Florida, proves to be correctly assigned to the Haematopodidae, but the genus *Palostralegus* is here considered a synonym of *Haematopus*. A humerus from the lower Pliocene Yorktown Formation in North Carolina is referred to *Haematopus* and is the earliest and only other Tertiary record of the family.

---

We have recently had an opportunity to examine the three specimens that presently make up the fossil record for the families Glareolidae and Haematopodidae. Although both these families are included in the suborder Charadrii of the Charadriiformes, within that group they are not closely related and it is only through an accident of history that we are forced to consider them together here.

Glareolidae

The Recent members of this family are entirely Old World in distribution, occurring in Africa, southern Europe, Asia, and Australia. Two subfamilies are recognized, the Glareolinae, or pratincoles, which are short-legged, aerially adapted forms with a swallow-like aspect, and the Cursoriinae, or coursers, which are long-legged and terrestrial. No fossils have previously been assigned to this family. We have found, however, that the fossil *Paractiornis perpusillus* Wetmore 1930, originally proposed as a new genus of diminutive Haematopodidae, actually pertains to the Glareolidae.

The type and only specimen of *Paractiornis perpusillus* is a left tarsometatarsus (MCZ 2191) lacking only the area of the intercotylar knob (Figs. 1b, d; 2b, c). It was collected 22 August 1929 by Erich M. Schlaikjer at Carnegie Hill, Agate fossil quarry, Sioux County, Nebraska, from the Harrison Formation, Arikarean land mammal stage, lower Miocene. Although Wetmore (1930:154) stated that the similarity between the type of *Paractiornis* and modern oystercatchers was "so close that the differences listed are seen only on careful scrutiny," to our eyes the differences were so great that from the beginning of our examination of the specimen we did not doubt that *Paractiornis* was incorrectly assigned to the Haematopodidae.

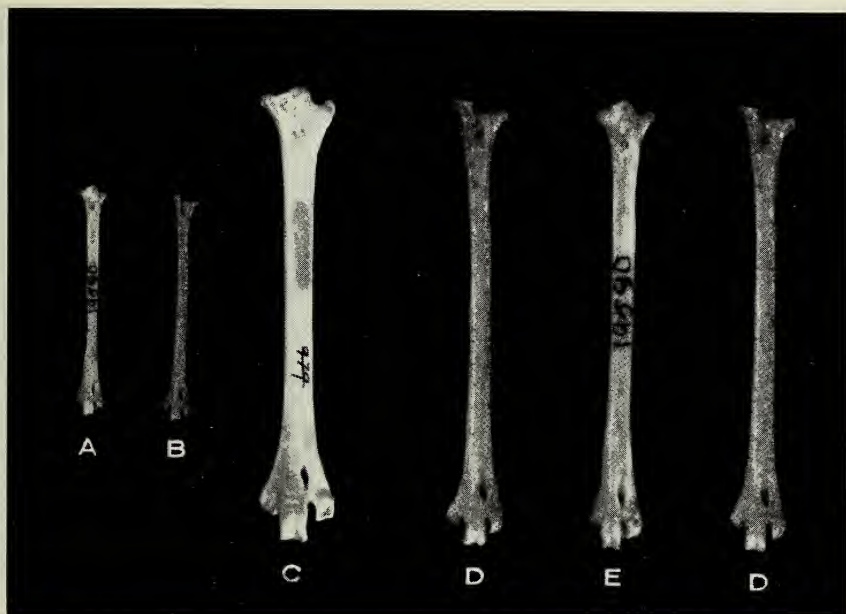


Fig. 1. Left tarsometatarsi in anterior view. *a* and *e*, *Glareola maldivarum*; *b* and *d*, *Paractiornis perpusillus*, holotype; *c*, *Haematopus palliatus*. *a-c* = 1 $\times$ ; *d-e* = 2 $\times$ . *d* = stereo pair.

As seen in Fig. 1, there is a great difference in size between the large and heavy-bodied modern *Haematopodidae* (all in the genus *Haematopus*), and *Paractiornis*, which was quite small and slender (the figures of *Paractiornis* in Wetmore 1930 are 2 $\times$ , not 1 $\times$  as stated in the caption). The proportions of the tarsometatarsus are also very different. In *Haematopus* the tarsometatarsus is stouter and the ends are much more expanded antero-posteriorly and latero-medially relative to the shaft than in *Paractiornis*. The outer hypotarsal ridge in *Haematopus* is much shorter than the inner ridge, whereas in *Paractiornis* these ridges are of about equal length, with a closed canal between them that is lacking in *Haematopus*. The ridge extending from the hypotarsus is nearly centered on the shaft in *Paractiornis* but is shifted more medially in *Haematopus*. The inner trochlea in *Haematopus* is rotated posteriorly farther towards the midline of the shaft and has a much larger and more posteriorly protruding wing. The outer trochlea is higher relative to the middle trochlea in *Haematopus* than in *Paractiornis*. The distal foramen is proportionately larger in *Paractiornis*. These differences are quite sufficient to remove *Paractiornis* from the *Haematopodidae* and it only remains to be seen with which group of shorebirds it can properly be affiliated.



Fig. 2. Holotype left tarsometatarsus of *Paractiornis perpusillus* (b and c, stereo pairs) compared with *Glareola maldivarum* (a and d). a-b = posterior views; c-d = medial views. All figures 2 $\times$ .

*Paractiornis* has none of the peculiarities of the tarsometatarsus of the Jacanidae (Olson, 1976). The distinctive, stout tarsometatarsus of the Thino-coridae has not the least resemblance to that of *Paractiornis*. The tarsometatarsus of the Chionididae is most similar to that of the Haematopodidae but is shorter and stouter and differs from *Paractiornis* in as many ways as does *Haematopus*. *Paractiornis* differs greatly from the Burhinidae, in which all three trochleae are more nearly in a single plane both proximo-distally and antero-posteriorly, the anterior surface of the shaft is more excavated, the shaft is almost triangular in cross section instead of square, and the distal foramen is very weakly developed. The Rostratulidae differ from *Paractiornis* in having the inner trochlea more elevated and more rotated inward towards the midline of the shaft, the inner trochlea with a larger wing, and the hypotarsus in medial view more abruptly set off from the shaft and less excavated on the medial side.

In the Charadriidae, the typical plovers (*Charadrius*, *Pluvialis*, etc.) differ greatly from *Paractiornis* in having the middle trochlea much more elongate, the inner and outer trochleae more elevated relative to the middle trochlea, and the inner trochlea more reflected. Among the lapwings, which are considered monogeneric by Bock (1958), but for which many generic



names are available, great variation exists in the conformation of the distal end of the tarsometatarsus. *Vanellus vanellus* is most similar to typical plovers, whereas "*Lobivanellus*" *miles* represents the greatest departure by having the middle trochlea in posterior view short, stout and square proximally, the inner trochlea more distally located and not nearly as reflected, and the outer trochlea more distally positioned. The possible taxonomic implications of this go beyond the scope of this paper but we believe that the inclusion of all the lapwings in a single genus, *Vanellus*, is probably an oversimplification. The modern lapwings are considerably larger, with much more slender and elongate tarsometatarsi, than *Paractiornis*. In none of these forms does the hypotarsal configuration agree with that of *Paractiornis*.

*Paractiornis* differs from the Scolopacidae and Phalaropodidae in having the distal foramen conspicuously larger, and the inner trochlea in medial view shorter and more rounded, lacking a posteriorly expanded wing. Even with the great variation in the Scolopacidae, there is still no genus in this large family that bears a close similarity to the combination of overall proportions of the tarsometatarsus and the positions of the trochleae in *Paractiornis*.

The Recurvirostridae differ markedly from *Paractiornis* in the greatly elevated inner trochlea with a well-developed wing, the relatively smaller distal foramen, the very elongate proportions, and in much greater size. *Dromas* (Dromadidae) differs in the same ways except that the inner trochlea is not as elevated as in the Recurvirostridae. Also, the external side of the hypotarsus is more excavated than in *Paractiornis*.

In the only remaining family of Charadrii, the Glareolidae, we find a very close agreement between *Paractiornis* and the modern forms of the genus *Glareola* (subfamily Glareolinae). In the Cursoriinae, the tarsometatarsi of *Cursorius* and *Rhinoptilus* are much longer and more slender than in *Paractiornis*, the distal foramen is smaller, and the outer trochlea is relatively smaller. The hypotarsi of *Cursorius* and *Rhinoptilus* differ considerably from each other and from *Paractiornis* as well, the ridges in *Cursorius* being shorter, and in *Rhinoptilus* longer, than in the fossil. *Pluvianus* differs from *Paractiornis* in having the inner trochlea much more medially flared, the distal foramen larger, and the hypotarsus with a very short outer ridge and a very long inner ridge tapering gradually into the shaft.

The only genus in the Glareolinae besides *Glareola* is the Australian *Stiltia*. Peter Ballmann (*in litt.* to Olson, 24 April 1978) informs us that the tarsometatarsus from a skeleton of *Stiltia isabella* in the Rijksmuseum van Natuurlijke Historie in Leiden measures 48 mm, or about 50% longer than in *Paractiornis* or *Glareola pratincola*, the latter being of about the same body

size as *Stiltia*. *Paractiornis* agrees exactly with the modern forms of *Glareola* in proportions, in the positions of the trochleae (particularly the lack of elevation and rotation of the inner trochlea), in the large distal foramen, in the lack of a distinct wing on the inner trochlea, in the conformation of the hypotarsus, and in the excavation of the medial side of the hypotarsus.

Lengths (in mm) of the various tarsometatarsi of *Glareola* compared are as follows: *Paractiornis perpusillus*, 30.8+ (slightly damaged); *Glareola pratincola*, 32.7–34.9 ( $n = 2$ ); *G. maldivarum*, 31.3; *G. nordmanni*, 38.2; *G. lactea*, 20.9–21.5 ( $n = 3$ ); *G. nuchalis*, 20.3–22.6 ( $n = 4$ ). *Paractiornis* differs from the similarly-sized *G. maldivarum* in having the inner trochlea more medially expanded, but this condition is matched in a specimen of *G. nordmanni*. It differs slightly from the specimens of modern *Glareola* in having the middle trochlea in medial view placed more anteriorly, extending somewhat beyond the line of the shaft, but in this respect it is closely approached by the smaller species *G. lactea* and *G. nuchalis*.

On comparing *Paractiornis perpusillus* with the Recent forms of *Glareola*, it is difficult to recognize any features in the fossil that may be used to separate it generically, the greatest difference being that the distal foramen is relatively larger than in any of the specimens of modern *Glareola* available to us. However, because of the considerable age of *Paractiornis*, it would be unwise to assume that the remainder of the skeleton was as similar to *Glareola* as is the tarsometatarsus. Furthermore, as Ballman (pers. comm.) is currently studying much more extensive fossil material of Glareolidae from the Miocene of Germany that may affect the status of *Paractiornis*, we tentatively retain *Paractiornis perpusillus* as an extinct genus and species closely allied to *Glareola*.

Because pratincoles are birds of open inland country, *Paractiornis perpusillus* now fits in much better with what is known of the ecological conditions of the early Miocene in Nebraska (Webb, 1977) than it did when it was considered a stunted oystercatcher. *Paractiornis* does present a zoogeographical anomaly in that the Glareolidae are otherwise unknown in the New World. However, as the species of *Glareola* are highly aerial and several of the modern species are migratory, tending to wander rather great distances, such a range extension is within reason. It is evident that glareolids once inhabited North America, from which they have disappeared since the early Miocene. It is to be hoped that the discovery of additional fossil specimens will allow us to determine more precisely when this took place.

#### Haematopodidae

The oystercatchers, Haematopodidae, are a nearly cosmopolitan group of large shorebirds that are usually malacophagous residents of coasts and

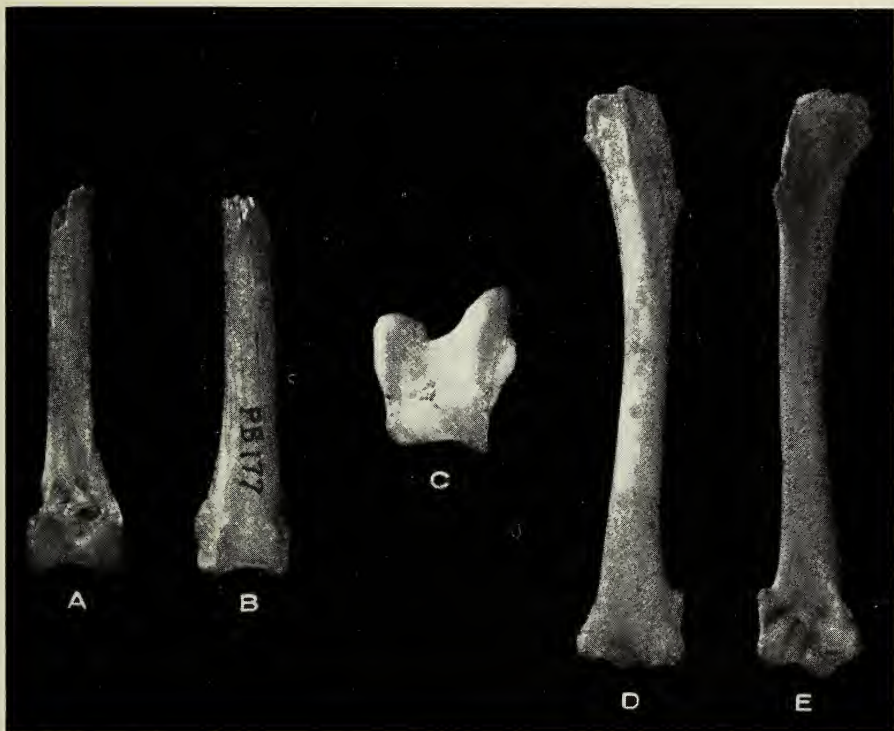


Fig. 3. *a-c*, *Haematopus sulcatus*, holotype right tibiotarsus (*a* = anterior, *b* = posterior, *c* = distal). *d*, *Haematopus* sp., right humerus USNM 215799 from Lee Creek, North Carolina, Yorktown Formation, Lower Pliocene. *a* and *b* = 1.5 $\times$ ; *c* = 2 $\times$ ; *d* and *e* = 1 $\times$ .

estuaries, although there are inland populations inhabiting wet meadows, rivers, and lakeshores in Europe, Asia, and New Zealand. The species-level systematics of the group is excessively complex and poorly understood, but all of the forms are morphologically quite similar and are placed in the single genus *Haematopus*.

#### *Haematopus sulcatus* (Brodkorb)

With the removal of *Paractiornis* from the Haematopodidae, only a single recorded fossil remains for the family, apart from subfossil and archeological specimens of modern species (Brodkorb, 1967). This is the distal end of a right tibiotarsus (Brodkorb collection no. 177) from the middle Pliocene Bone Valley Formation (probably Hemphillian land mammal stage) near Brewster, Polk County, Florida (Fig. 3a-c). Brodkorb (1955) described this specimen as a new genus and species, *Palostralegus sulcatus*. We com-



pared the type with all other families of Charadrii and confirmed that it is correctly referred to the Haematopodidae. This is particularly evident on the basis of the intercondylar sulcus in distal view being narrow, sharply perpendicular to the external condyle but sloping gradually into an anteriorly elongated internal condyle (Fig. 3c). In other Charadrii the internal margin of this sulcus is more perpendicular to the internal condyle.

Further comparison of the type with 25 skeletons representing five Recent forms of *Haematopus* reveals several inconsistencies with the generic diagnosis of *Palostralegus* (Brodkorb, 1955:20). The deeply excavated intercondylar sulcus of *Palostralegus* reported by Brodkorb is closely approached by certain individuals of *H. ater* and *H. leucopodus*. The ossified supratendinal bridge in the fossil also was supposed to distinguish it from *Haematopus*. We find, however, that in Recent *Haematopus* the tendinal bridge may be variably ossified within and between species. In a pair of *H. palliatus* taken together in Florida, the bridge is ossified in the male and unossified in the female. On the other hand, the bridge is ossified in all our specimens of *H. leucopodus*, and unossified in all specimens of *H. ater*. In any case, the condition of the supratendinal bridge is evidently worthless as a generic character. In the fossil the tendinal groove above the supratendinal bridge is deeper than in Recent species but not narrower as stated by Brodkorb (1955). The width of this "groove" cannot always be determined in Recent forms because in many specimens no impression whatever is apparent on the shaft. The internal ligamental prominence, said by Brodkorb (1955:20) to be "slightly higher and slightly better developed" in the fossil, is extremely variable in size, shape and position in the Recent forms.

Re-examination of the supposed specific characters of *P. sulcatus* given by Brodkorb (1955:21) proves many of them to be invalid. The width through the condyles is not less than in *H. palliatus* or *H. bachmani* (Table 1). The external ligamental prominence, said to be "situated higher on shaft and more pronounced" in *P. sulcatus*, is indeed more pronounced than in *H. palliatus* or *H. bachmani*, but not more so than in *H. ater*, *H. ostralegus*, or *H. leucopodus*. The position of this structure on the shaft of the fossil is the same as in living forms. The internal condyle is deeper in the fossil than in *H. ostralegus* or *H. leucopodus*, as stated, but is not deeper than in *H. palliatus*, *H. bachmani*, or *H. ater*. The groove for *M. peroneus profundus*, supposedly deeper in the fossil than in *H. palliatus* or *H. bachmani*, is in fact equalled in depth by certain individuals of *H. palliatus*, *H. ater*, and *H. leucopodus*.

Characters given by Brodkorb which seem to be valid for the species *P. sulcatus* are the stout shaft (see Table 1), the more pronounced tendinal groove, and the deep intercondylar sulcus. These characters, however, seem insufficient to separate the species at the generic level from *Haemat-*

Table 1. Measurements (mm) of Haematopodidae; means in parentheses.

	Humerus				Tibiotarsus		
	Length from distal end to distal end of scar for M. pectoralis	Least width of shaft	Least depth of shaft	Distal width	Least width of shaft	Least depth of shaft	Distal width
<i>Haematopus sulcatus</i> PB 177	—	—	—	—	4.3	3.6	8.3
<i>Haematopus</i> sp. USNM 215799	62.6	6.2	4.6	14.9	—	—	—
<i>H. ostralegus</i> (1 ♂, 1 ♀)	51.8–52.5	5.0–5.1	3.6–4.0	11.6–12.2	3.3	2.9	8.4
<i>H. palliatus</i> (2 ♂, 2 ♀)	58.7–61.3 (59.5)	5.4–5.6 (5.5)	3.9–4.1 (4.0)	13.1–13.5 (13.4)	3.8–3.9 (3.9)	3.1 (3.1)	7.8–8.7 (8.2)
<i>H. bachmani</i> (1 ♂, 2 ♀)	54.8–60.2 (57.8)	5.3–6.0 (5.7)	3.8–4.4 (4.2)	12.8–14.1 (13.6)	3.7–4.0 (3.8)	3.2–3.4 (3.3)	8.3–9.4 (8.9)
<i>H. ater</i> (3 ♂, 6 ♀, 2 ♀)	57.8–61.9 (59.8)	5.6–6.2 (5.9)	3.9–4.6 (4.2)	14.3–15.5 (15.0)	3.6–4.3 (4.0)	3.0–3.6 (3.3)	8.8–10.3 (9.6)
<i>H. leucopodus</i> (3 ♂, 2 ♀)	51.5–56.3 (53.8)	5.1–5.5 (5.3)	4.0–4.3 (4.1)	13.2–13.7 (13.5)	3.8–4.0 (3.9)	2.9–3.0 (2.9)	8.6–9.1 (8.8)



opus. Therefore, *Palostralegus* Brodkorb 1955 becomes a synonym of *Haematopus* Linnaeus 1758 and its only species should now be known as *Haematopus sulcatus* (Brodkorb).

### *Haematopus* sp.

Further to extend the Tertiary history of oystercatchers, we report here a second fossil specimen referable to *Haematopus*. This is a right humerus (USNM 215799) lacking the proximal end (Fig. 3d-e). It was received from Peter J. Harmatuk on 10 April 1975 and was collected from lower Pliocene deposits of the Yorktown Formation at Lee Creek, south side of Pamlico River, near Aurora, Beaufort County, North Carolina (see Olson, 1977). Microfossils in a matrix sample from this specimen were considered as being "probably lower Yorktown" (Thomas G. Gibson, pers. comm.).

The specimen differs from living species of *Haematopus* only in having a shallower olecranal fossa and tricipital groove. However, it is closely approached in this character by *H. leucopodus* and certain individuals of *H. ostralegus* and *H. palliatus*. In addition, the fossil has a narrow but distinct crescentic groove on the distal surface of the bicipital crest, lacking in all the forms examined except *H. leucopodus*. The fossil has a more rounded (less elongated) anterior articular ligament than observed in other specimens except certain individuals of *H. ater*.

The brachial depression is more deeply excavated, especially in its disto-medial portion, than in any of the specimens examined except certain individuals of *H. ater* and *H. ostralegus*. In size the fossil is very slightly larger than in the largest species of Recent *Haematopus* examined (*H. ater*) and it is considerably more robust and larger than in *H. palliatus*, the form occurring in the same area today (see Table 1).

As the present specimen differs so little from Recent *Haematopus*, its assignment to that genus is justified. It provides the earliest record for *Haematopus* and the Haematopodidae and strengthens our contention that the specimen from Bone Valley should also be included in this genus. Because the humerus from North Carolina cannot be compared directly with *Haematopus sulcatus*, which is based on a tibiotarsus, the specimen does not warrant any further refinement of its nomenclatural status and we list it simply as *Haematopus* species.

### Comparative Material Examined

For species-level comparisons, skeletons of the following taxa from the collections of the National Museum of Natural History (USNM) were examined: *Glareola maldivarum* 1, *G. nordmanni* 1, *G. lactea* 3, *G. nuchalis* 4, *G. pratincola* 2; *Haematopus ostralegus* 2, *H. palliatus* 4, *H. bachmani* 3, *H. ater* 11, *H. leucopodus* 5.

In addition, the following genera and species were used in determining the familial identity of the fossils studied in this paper: *Jacana jacana*, *Nycticryphes semicollaris*, *Rostratula benghalensis*, *Vanellus vanellus*, *V. miles*, *V. chilensis*, *V. albiceps*, *V. coronatus*, *V. cayanus*, *V. crassirostris*, *V. tectus*, *V. armatus*, *V. tricolor*, *V. senegallus*, *Pluvialis dominica*, *Charadrius vociferus*, *Bartramia longicauda*, *Numenius minutus*, *Limosa fedoa*, *Tringa flavipes*, *Tringa solitaria*, *Actitis macularia*, *Catoptrophorus semipalmatus*, *Heteroscelus incanum*, *Aphriza virgata*, *Limnodromus griseus*, *Capella gallinago*, *Philohela minor*, *Limnocryptes minimus*, *Calidris canutus*, *C. melanotos*, *Micropalama himantopus*, *Tryngites subruficollis*, *Philomachus pugnax*, *Recurvirostra americana*, *Himantopus mexicanus*, *Steganopus tricolor*, *Phalaropus fulicarius*, *Dromas ardeola*, *Burhinus vermiculatus*, *Rhinoptilus africanus*, *Cursorius temminckii*, *Pluvianus aegyptius*, *Attagis malouinus*, *Chionis alba*.

### Acknowledgments

We are particularly indebted to Pierce Brodkorb, University of Florida, and Raymond A. Paynter, Jr., Museum of Comparative Zoology (MCZ), Harvard University, for lending the type specimens that made this study possible. For collecting and donating the fossil specimen of *Haematopus* from North Carolina, and for his indefatigable work in collecting other vertebrate remains at Lee Creek, we are most grateful to Peter J. Harmatuk. The photographs are by Victor E. Krantz. For their helpful comments on the manuscript we thank Peter Ballmann, John Farrand, Jr., and Clayton E. Ray.

### Literature Cited

- Bock, W. J. 1958. A generic review of the plovers (Charadriinae, Aves). *Bulletin of the Museum of Comparative Zoology* 118(2):26-97.
- Brodkorb, P. 1955. The avifauna of the Bone Valley Formation. *Florida Geological Survey, Report of Investigations*, Number 14:1-57.
- . 1967. Catalogue of fossil birds: Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). *Bulletin of the Florida State Museum, Biological Sciences* 11(3):99-220.
- Olson, S. L. 1976. A jacana from the Pliocene of Florida (Aves: Jacanidae). *Proceedings of the Biological Society of Washington* 89(19):259-264.
- . 1977. A great auk, *Pinguinis*, from the Pliocene of North Carolina (Aves: Alcidae). *Proceedings of the Biological Society of Washington* 90(3):690-697.
- Webb, S. D. 1977. A history of savanna vertebrates in the New World. Part 1: North America. *Annual Review of Ecology and Systematics* 8:355-380.
- Wetmore, A. 1930. Two fossil birds from the Miocene of Nebraska. *Condor* 32(3):152-154.

(SLO) Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (DWS) Department of Geosciences, University of Arizona, Tucson, Arizona 85721.